DETAILED COMPARISONS OF THE DENTITIONS OF EXTANT HEXANCHID SHARKS AND TERTIARY HEXANCHID TEETH FROM SOUTH AUSTRALIA AND VICTORIA, AUSTRALIA (SELACHII: HEXANCHIDAE)

By Noel R. Kemp
Tasmanian Museum, G.P.O. Box 1164M, Hobart, 7001, Australia

Abstract

In extant hexanchid sharks except for (usually) a bigger primary cusp, isolated teeth of a given size of the smaller species *Hexanchus vitulus* (Springer and Waller) may be confused with those of *H. griseus* (Bonnaterre). This specific size difference has significance in the fossil record. *Heptranchias perlo* (Bonn.) differs in its more slender and relatively larger primary cusp with basal denticles (not serrations as in *Hexanchus*) on its mesial margin and fewer crownlets increasing and then decreasing in size distally. *Notorynchus cepedianus* (Péron) differs mainly in its more robust primary cusp and crownlets which are fewer in number than in *Hexanchus* and which decrease evenly in size distally, like *Hexanchus*. Californian specimens of *Notorynchus* are included in the monotypic *N. cepedianus* until the taxonomic significance of the variability of the upper medial teeth is established and defined. *N. cepedianus* is recorded from the fossil record for the first time. *Heptranchias haswelli* Ogilby is regarded as a *species inquirenda*. *Hexanchus agassizi* Cappetta is expanded to include the Eocene *Hexanchus* teeth from South Australia. *Heptranchias howellii* (Reed) from the South Australian Eocene and *Notorynchus primigenius* (Agassiz) from the Victorian Miocene are recorded and described from Australia for the first time.

Introduction

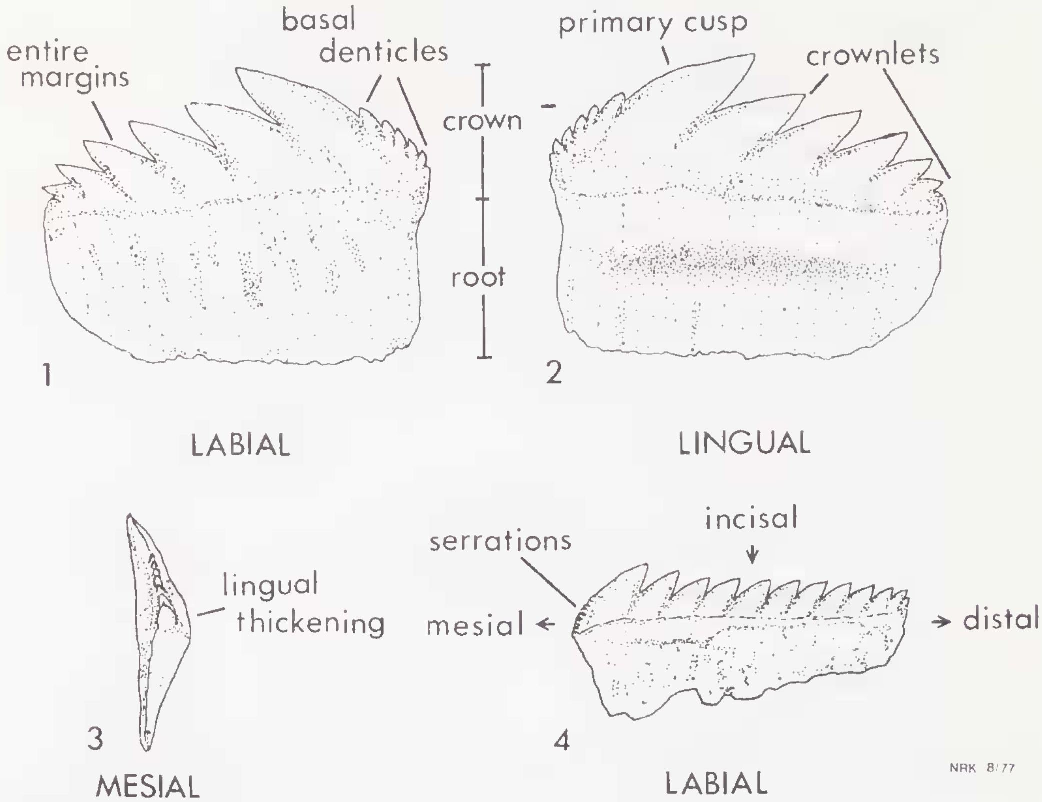
The sixgill and sevengill sharks of the family Hexanchidae, although a relatively small group, are well represented in the fossil record, especially outside Australia, for example Woodward (1886), Jordan (1907), Leriche (1910, 1927, 1957) and are common in modern seas, for example Garman (1913), Bigelow and Schroeder (1948), Whitley (1968), Bass, D'-Aubrey and Kistnasamy (1975). Taxonomically, however, they are not a stable group (see below).

Less than a dozen fossil hexanchid teeth have been described from the Australian fossil record (Pledge, 1967; Kemp, 1970). Three teeth and several fragments from the Eocene of South Australia were assigned by Pledge (1967) to *'Notidanus' serratissimus* Ag., *'N'* cf. *serratissimus* and *'N'* ? *serritissimus*. The three fragments from the Miocene of Victoria were described by Kemp (1970) as *Notorynchus* cf. *primigenius*. In light of recent publications (Welton, 1974; Cappetta, 1976) and with the recovery of further specimens from the South Australian Eocene during the last decade, the present study shows that the three extant genera are represented in the South Australian and Victorian Tertiary material.

Compagno (1973) lists two families in the suborder Hexanchoidei: Hexanchidae, with two genera, *Hexanchus* and *Notorynchus* and Heptranchidae with the monotypic genus *Heptranchias*. He based this separation of *Heptranchias* into its own family on a suggestion by Dr Shelton P. Applegate 'because of many differences in cranial and external morphology between it and the other hexanchoids (*Hexanchus* and *Notorynchus*)' (Compagno, 1973:33). Recently Bass *et al.* (1975) suggest that more detailed anatomical studies of the six- and sevengill sharks may show that the smaller species of *Hexanchus, H. vitulus*, may have more in common with *Heptranchias perlo* than with the larger species, *Hexanchus griseus. H. griseus*, on the other hand, may have more in common with *Notorynchus cepedianus*. Until these suggestions are confirmed or repudiated by further detailed work the suprageneric classification adopted here is that of Patterson (1967).

Terminology

The tooth types medials, laterals and posteriors are used in the sense of Applegate (1965a). The faces of a tooth are termed labial and lingual and the margins mesial and



Figures 1-4—Terminology.
1-3. *Notorynchus cepedianus* (Péron), lower right second lateral tooth (Figs. 1, 2, x2; Fig. 3, x1·5).
4. *Hexanchus agassizi* Cappetta, lower left lateral of about fourth, fifth or sixth row (x1·5).

distal as defined by Hoojier (1954). In the cockscomb-like dentition of the hexanchids the larger primary cusp is followed by a number of crownlets (Applegate, 1965b). The mesial margin of the primary cusp may be serrated, or, if the serrations are relatively large, they are termed basal denticles. A character of the family is the presence of one series of functional teeth in both jaws except for the upper medials which have two or three and the posteriors of both jaws which have two to four functional series. The description of dentition of *Hexanchus griseus* is given in detail as a datum for the diagnoses of the other species.

Abbreviations

The following abbreviations are used: AMS, Australian Museum, Sydney; AUGD, University of Adelaide, Department of Geology; CM, Canterbury Museum, Christchurch, New Zealand; MUGD, University of Melbourne, Department of Geology; NMV, National Museum of Victoria, Melbourne; NZNM, National Museum of New Zealand, Wellington; RJFJ, private collection of Dr R. J. F. Jenkins, South Australia; SAMD, South Australian Department of Mines; SAM, South Australian Museum, Adelaide; TFF, private collection of Mr T. F. Flannery, Beaumaris, Victoria; USNM, United States National Museum, Washington.

Systematics

Order HEXANCHIFORMES
Suborder HEXANCHOIDEI
Family HEXANCHIDAE

The Hexanchidae are characterized by six or seven gill-openings and heterodont dentition, that is the teeth are of dissimilar shape both within and between the two jaws. Except for another two families all other sharks have only five gill openings.

The Chlamydoselachidae, or frill shark, of which only one specimen has been recorded from Australian waters, in 1976 (J. R. Paxton, pers. comm.), has a terminal mouth compared with the subterminal mouth of all other sharks and six gill openings with the first opening continuous across the throat. The remaining five openings are interrupted on the ventral surface. The dentition of *Chlamydoselachus*, the single genus of the family, is homeodont, that is all the teeth are of similar shape both within and between the two jaws.

The Pristiophoridae, or saw sharks, has a sixgill genus, *Pliotrema*, which has yet to be found in Australian waters. It is easily separated from the sixgill hexanchid species by its two dorsal fins, rostral snout with barbells and marginal teeth, homeodont dentition and no anal fin. The hexanchids have only one dorsal fin, no rostral snout and possess an anal fin.

Main characters

One dorsal fin, always posterior to pelvics; anal fin present; caudal fin with a definite lobe and well marked subterminal notch; precaudal pit absent; six or seven gill-openings not connected ventrally, last gill opening in front of and extending below pectoral origin; spiracle present but small; nictitating membrane absent; upper labial furrow absent, lower labial furrow present, developed to varying degrees.

Dentition heterodont: upper jaw, teeth with slender primary cusp and a variable number of small crownlets; small medial tooth present or absent; lower jaw, teeth basically trapezoidal in outline and multicusped; small medial tooth present. Small undifferentiated posterior teeth present in both jaws.

As all species of hexanchids possess a similar pavement-like dentition formed by the posteriors in both jaws and as they are rarely recognized in the fossil record, teeth of this type are omitted in the following descriptions and diagnoses.

Genera

Rafinesque (1810) erected two genera, *Hexanchus* and *Heptranchias*, based on six- and sevengill sharks respectively. Cuvier (1817, *fide* Bigelow and Schroeder, 1948) included both of these genera in his new genus *Notidanus*. This genus also came to include another sevengill shark, *Notorynchus*, both before and after Ayres (1855) described it as a new genus. Subsequent studies showed that the three genera of Rafinesque and Ayres were valid and Cuvier's *Notidanus* has not been used for extant sharks for more than half a century. Palaeontologists have until recently used *Notidanus* as an encompassing genus, for example Leriche (1957), Casier (1966), Cappetta *et al.* (1967) (*fide* Cappetta 1970), Pledge (1967), as it was widely held that separation of the genera of hexanchids was only possible on the basis of the anatomy of their soft parts. A number of authors, however (Applegate 1965b; Waldman 1970; Welton 1974; Cappetta 1975) have noted some of the salient dental differences, mainly in the lower lateral teeth, between these three genera. Antunes and Jonet (1969), in describing Miocene teeth from Portugal, include in the family Hexanchidae only two genera, *Hexanchus* Rafinesque and *Heptranchias* Rafinesque. They include *Notorynchus* Ayres in the latter genus but give no reason for this.

As set out in the key below the sixgill genus is readily separated from the two sevengill genera which differ from each other in the shape and size of their snouts. The descriptions under each genus further differentiates them on their dental characteristics.

KEY TO LIVING GENERA

(After Bigelow and Schroeder, 1948).

1A Six gill-openings . . . . *Hexanchus*

1B Seven gill-openings 2

2A Head narrow; snout tapering; horizontal diameter of eye considerably greater than distance between nostrils . . . . *Heptranchias*

2B Head broad; snout broadly rounded; horizontal diameter of eye considerably smaller than distance between nostrils . . . . *Notorynchus*

Genus *HEXANCHUS* Rafinesque, 1810

Hexanchus Rafinesque, 1810:14; type species *Squalus griseus* Bonnaterre, 1788.

Generic Diagnosis

Six gill-openings, not joining across the ventral surface; lower labial furrow well developed.

No central medial tooth in upper jaw; lower laterals with 5 to 6 crownlets in specimens of about 500 mm total length, increasing up to 10 to 12 in specimens of about 4000 mm total length. Characters otherwise those of family.

Living Species

Two species of the genus *Hexanchus* are recognized (Springer and Waller, 1969), *H. griseus* and *H. vitulus*. The larger species, *H. griseus*, which reaches sexual maturity at about 4500 mm has 5 lower lateral teeth on each side of the jaw. The smaller species, *H. vitulus*, which reaches sexual maturity at about 1400 mm to 1750 mm has 6.

KEY TO LIVING SPECIES OF *HEXANCHUS* (After Springer and Waller, 1969)

1A Five rows of large trapezoidal teeth on each side of the lower jaw . . . . *griseus* Bonnaterre, 1788

1B Six rows of large trapezoidal teeth on each side of the lower jaw . . . . . . *vitulus* Springer and Waller, 1969

Bass *et al.* (1975) list a number of apparent differences between the two species. One of these differences, relating to the shape of the symphyseal region of the upper jaw, may be a post-mortem artifact caused either by drying of the removed jaws or by fixation of *in situ* jaws in spirit collections. In *H. griseus* the upper medial teeth are set approximately in line with the general curvature of the jaw whereas in *H. vitulus* the upper medials bulge markedly forward from the line of the rest of the jaw (Bass *et al.*, 1975:7, Pl. 3A, 3B).

In three of the five jaws of *H. griseus* in the present study, AMS I19110-001, USNM 188048 and NMV A235 the upper medials bulge forward exactly as shown by the South African *H. vitulus* (Bass *et al.*, 1975, Pl. 3B). In one specimen of *H. vitulus* (USNM 112600) the upper medials do protrude but only slightly, much less so than in the Victorian *H. griseus*. These jaws are still *in situ*, the shark being preserved in the National Museum of Victoria's spirit collection.

Hexanchus griseus (Bonnaterre, 1788)*

* The date of Bonnaterre's *Squalus griseus* is often quoted in post-1948 literature as 1780. This error seems to stem from Bigelow and Schroeder's (1948) incorrect date on page 80. The correct date is used on pp. 78 and 85.

Bluntnose sixgill shark, Mud shark, Cow shark

(Plate 12, figures 1-4)

Squalus griseus Bonnaterre, 1788: 9.

Notidanus griseus (Cuvier, 1817); Agassiz, 1835, Pl. E, figs. 2-4; 1838: 92; 1843: 218.

Notidanus griseus Cuvier, 1817; Agassiz, 1870: 397.

Notidanus griseus (Linné-Gmelin, 1788); Leriche, 1910: 225, Fig. 70.

Hexanchus griseus (Bonnaterre, 1788); Clemens and Wilby, 1946: 52, Fig. 12; Parrott, 1958: 83, text fig.; Whitley, 1968: 5; Welton, 1974: 2, Pl. 1E; Bass *et al.*, 1975: 8, Fig. 5, Pl. 1, 3A.

Hexanchus griseus (Bonnaterre, 1780); Bigelow and Schroder, 1948. 80 (*part*), Figs. 8, 9 (*non* Fig. 9A = *H. vitulus*, S. Springer, pres. comm.); Lynch 1963: 295, Figs. 1-5; Springer and Waller, 1969: 169, Figs. 2B, 5-7.

Hexanchus griseum (Bonnaterre, 1788); Springer and Garrick, 1964, Table 1.

? *Isurus oxyrhinchus* Rafinesque, 1810; Antunes and Jonet, 1969: 136 (*part.*), Pl. 7, fig. 22 (*non* Fig. 24).

(*non*) *Hexanchus* cf. *griseus* (Bonnaterre, 1780); Antunes and Jonet, 1969: 130, Pl. 4, figs. 1-3.

Extant Material Examined. 2187 mm female taken in 200 m off Port Fairey, Vict., Mar., 1963 (NMV A235, spirit collection); jaws of 4250 mm specimen taken in 450 m off Norah Head, N.S.W., June, 1976 (AMS I19110-001); photographs of jaws of 4330 mm female, Gulf of Mexico (USNM 188048) (Springer and Waller, 1969: 169); photographs of tooth sets (Applegate, 1965a) of one side of jaws of eight specimens ranging from 696 mm to 4346 mm from California, U.S.A.

Dentition

Dental formula of AMS I191100-001 (Pl. 12, figs. 1-4) $\frac{\mathrm{P8\ L9\ M4\ L9\ P8}}{\mathrm{P8\ L6\ M1\ L6\ P9}}$. Numerical variation is restricted to the upper laterals, from 7 to 9 rows on each side. The number of upper and lower medials and lower laterals is constant in the above material and in the figured dentitions e.g. Bigelow and Schroeder, 1948, Fig. 8E; Bass *et al.*, 1975, Pl. 1. Bigelow and Schroeder (1948: 82, footnote) record a small Mediterranian specimen in which there is no lower medial tooth.

In all teeth the crown and its subdivisions—cusps, crownlets, basal denticles or serrae—are equally biconvex labio-lingually. The root is simple, not branching, approximately square or trapezoidal in outline and is wedge-shaped, thinning from the base of the crown to the basal margin.

Upper Jaw

Medials. Four rows with lanceolate crowns curved away from the symphysis, two rows on each side. Margins entire except in large specimens about 2-3 m or more in length which may have margins serrated or even with basal denticles. Root rhomboidal in outline and with a pronounced thickening labio-lingually.

Laterals. From 7 to 9 rows on each side of the jaw. Teeth of first row about as high as broad with a slightly inclined, curved primary cusp and 1 or 2 crownlets distally. Basal half of mesial margin serrated. Teeth of last rows about twice as broad as high with a more inclined and almost straight primary cusp only slightly bigger than the first crownlet; 3 to 6 more crownlets decreasing evenly in size distally. Basal two-thirds of mesial margin of tooth finely serrated. Other laterals grading in size and shape between these end members. Teeth from specimens of about a metre or less in length show less variation. Mesial margin may be entire and distal margin may have only small crownlets, perhaps only 2 or 3, even in rows nearest jaw articulation.

Lower Jaw

Medial. Tooth about as high as broad with from 3 to 6 laterally directed secondary cusps and either with or without a central cusp. Central cusp when present may be bifurcated and symmetrical or single and asymmetrical. Root approximately square in outline.

Laterals. Six rows on either side of the medial, lower laterals largest in a set of jaws; basically trapezoidal in shape and about twice as broad as high. Crown divided into a primary cusp only slightly bigger than the following crownlets which decrease evenly in size distally. From 6 to 8 or 9 crownlets in specimens about 2 m or less in length. In larger specimens the number of crownlets increases from 9 to 10 in first rows through to 10 to 12 in last rows. Inclination of crownlets more or less constant throughout laterals. Mesial margins smooth in small specimens. Basal two-thirds finely serrated in specimens about 1·5 m in length and more coarsely serrated in larger specimens. Serrations coarsest midway along mesial margin, serrations of first rows coarser than those of last. Root more or less rectangular in outline.

Discussion. In all hexanchids the upper lateral rows towards the jaw articulation are similar in shape to their lower equivalents. Common to the three genera however are differences which may serve to differentiate these respective tooth types. In the uppers the primary cusp may be relatively higher and broader than in the lowers. The mesial margin of the primary cusp is usually more than half the length of the upper tooth whereas in the lowers it is less than half and often near one-third, i.e. the primary cusp in the uppers is more centrally placed. There are always more crownlets in the lowers than in the uppers—this may be less significant with isolated teeth.

Three Upper Miocene hexanchid teeth are referred to *Hexanchus* cf. *griseus* by Antunes and Jonet (1969). The crowns of the two upper medials (Antunes and Jonet, 1969, Pl. 4, figs. 1, 2) are too slender and too obliquely curved to be *H. griseus.* The lower lateral tooth (Antunes and Jonet, 1969, Pl. 4, fig. 3) has a large primary cusp with reasonably coarse serrations on the mesial margin followed by six well developed crownlets. The low number and relatively large size of the crownlets compared with the size of the tooth strongly suggests a notorynchid tooth, probably *Notorynchus primigenius.* The tooth figured by Antunes and Jonet (1969, Pl. 7, fig. 22) as an abnormal *Isurus oxyrinchus* is very similar to an upper medial in an Australian *Hexanchus griseus* (AMS I19110-001, Pl. 12, fig. 2) in its size, shape and obliquity of the crown and the presence of small denticles at the base of the mesial margin and is probably referable to that species.

Distribution. Hexanchus griseus occurs in the Atlantic, Pacific and Indian Oceans and in the Mediterranean Sea inhabiting both tropical and temperate water (Bigelow and Schroeder, 1948). Bass *et al.* (1975) note that *H. griseus* and *Hexanchus vitulus* of equivalent size occupy different ranges. The young of *H. griseus* inhabit temperate regions while *H. vitulus* occupies the tropical areas.

H. griseus is often taken on long lines at about 200 m and as deep as 1400 m; it is also known from shoal waters (Bigelow and Schroeder, 1948). Springer and Waller (1969) suggest that it lives on the continental slopes at depths of 350 m or more, occasionally moving into shallower waters. Vaillant recorded a 4·5 m female being taken in shallow water on a bar off Archachan in the Bay of Biscay (*fide* Springer and Waller, 1969).

Hexanchus vitulus Springer and Waller, 1969
Bigeye sixgill shark
(Plate 12, figure 5)

Hexanchus vitulus Springer and Waller 1969: 160, Figs. 1, 2A, 3, 4; Bass *et al.*, 1975: 9, Fig. 6, Pl. 2, 3B.

Extant Material Examined. Photographs of teeth *in situ* of two dried jaws: no data (USNM 110900); 1630 mm female taken at 275 m, Bahamas, 1948 (USNM 112600).

Dentition

Tooth counts (Springer and Waller, 1969; Bass *et al.*, 1975) show a range of $\frac{\mathrm{P8\text{-}9\ L7\ M4\ L7\ P9}}{\mathrm{P3\text{-}5\ L5\ M1\ L5\ P5}}$. These data represent at least ten jaws which suggests that the number of upper laterals is constant (cf. *H. griseus*) and numerical variation is restricted to the posteriors of both jaws.

Diagnosis. Teeth small, basically similar to those of *H. griseus.*

Upper Jaw

Medials. Crowns may be more curved than in *H. griseus* and margin between top of root and base of crown, distally, more strongly arcuate.
Laterals. Similar to *H. griseus* but primary cusp proportionately bigger than distal crownlets and mesial margin more finely serrated.

Lower Jaw

Medial. Similar to medial of *H. griseus* including variability of central cusp.
Laterals. Primary cusp usually proportionately bigger than distal crownlets compared with *H. griseus.*

Discussion. An important feature demonstrated by the dentition of these two species of *Hexanchus* is that of size difference. The largest tooth from a large, sexually mature *H. vitulus* rarely exceeds 22 to 25 mm whereas that from a large, sexually mature *H. griseus* could be from 45 to 50 mm in length. Isolated teeth of the same size and of the same jaw position could be difficult to refer to one species or the other. However, with a random sample of teeth such as in the fossil record, if the two species were present at the time of deposition one would expect a size difference in the teeth to be apparent thus demonstrating the existence of the two species.

The size difference could also be interpreted as simply being teeth from juvenile and adult specimens of *H. griseus.* Allometric growth patterns would enable the differentiation of a tooth of a juvenile *H. griseus* from a tooth of an adult *H. vitulus*, for example there would be more crownlets on the *H. vitulus* tooth than on the similar-sized *H. griseus* specimen.

Empirically though, in any one species of fossil teeth there is a tendency to size clustering, especially in smaller samples. (In contrast, however, in the National Museum of Victoria's collection of sharks' teeth there are 3-4000 teeth of *Isurus hastalis* (Agassiz, 1838) and a size range of juvenile to adult teeth is apparent, but, the majority of specimens represent large sharks; a collecting bias may favour this size distribution). There are many variables involved to produce this result but one dominating factor could be that the teeth shed by living sharks are insignificant in the fossil record compared with those from a dead adult. If an adult dies, immediately there is the potential of hundreds of teeth and crowns being preserved. In *Notorynchus cepedianus* for example there would be about one hundred while in a species such as *Odontaspis taurus* Rafinesque, 1810—the grey nurse shark, in Australia—it could be as high as three to four hundred.

Distribution: H. vitulus has been recorded from the south-eastern Indian Ocean between Kenya and Natal (Bass *et al.*, 1975), from Florida—Gulf of Mexico-West Indies region—and from the Philippines (Springer and Waller, 1969). Müller and Henle's (1841) records of *H. griseus* from the Atlantic and Mediterranean may well include *H. vitulus* as they state that their specimens had 5 or 6 rows of broad teeth in the lower jaws (*fide* Springer and Waller, 1969).

H. vitulus is a tropical to subtropical demersal species being taken at depths between 90 and 600 m with one specimen being netted just off shore in Natal. It is rarely taken in temperate waters (Bass *et al.*, 1975).

Hexanchus agassizi Cappetta, 1976

Plate 14, figures 4-11; Plate 15, figures 1-3

Hexanchus agassizi Cappetta, 1976: 553, Pl. 1, figs. 5-8.

Notidanus serratissimus Agassiz: Woodward, 1886: 216, Pl. 6, figs. 24, 25, 26 (*non* fig. 23); Woodward, 1899: 6, Pl. 1, fig. 7 (*non* fig. 6); Casier, 1966: 44, Pl. 1, figs. 10-12 (*non* figs. 1-9).

'Notidanus' serratissimus Agassiz: Pledge, 1967: 140, Pl. 1, fig. 1.

'Notidanus' cf. *serratissimus* Agassiz: Pledge, 1967: 140, Pl. 1, fig. 2.

'Notidanus' ? serratissimus Agassiz: Pledge, 1967: 140, fig. 3, two top specimens only (*non* bottom two specimens).

Fossil Material Examined. Four teeth (SAMD V34; UAGD F17262; SAM P19552, P19643) Vand a dozen broken teeth and fragments (SAMD V60; SAM P19552).

Occurrence. Knight Formation equivalents, E and WS, Naracoorte No. 5 Bore, 135-145 m, Naracoorte, South Australia; Blanche Point Marl at Blanche Point and Port Noarlunga, South Australia.

Age. Knight Formation equivalents, Middle Eocene; Blanche Point Marl, Upper Eocene (Pledge, 1967).

Diganosis. Teeth up to 23 mm long, very similar to those of the extant *H. vitulus* but with the primary cusp nearer in size to the distal crownlets. The primary cusp of the uppers may be more attenuated and sinuous than in *H. vitulus.*

Description. One tooth (Pl. 15, fig. 2 = Pledge, 1967, Pl. 1, fig. 1) shows clearly the main characters of *H. agassizi:* the crownlets which decrease evenly in size distally from the slightly larger primary cusp with its finely serrated mesial margin; the slight lingual concavity of the tooth when viewed incisally. The length of the specimen is twice that stated in Cappetta's (1976) diagnosis. As with Cappetta (1976) upper teeth are poorly represented in the collection on hand.

One almost complete tooth (Pl. 14, fig. 4) possesses the slender, sinuous primary cusp with a serrated mesial margin and the second distal crownlet, the first crownlet being lost. The presence of only 2 crownlets suggests that the tooth is from the first or second row of the laterals. The two incomplete crowns (Pl. 14, figs. 5, 6) show that the difference in size between the primary cusp and the first crownlet is less marked than in the equivalent teeth of the extant *H. vitulus*.

A broken lower tooth possessing only the primary cusp, first crownlet and part of the root (Pl. 14, figs. 10, 11) has one denticle on the base of the medial margin of the first crownlet. This feature has not been seen before in an hexanchid tooth and probably represents an individual variation.

A well preserved tooth (Pl. 15, fig. 1 = Pledge, 1967, Pl. 1, fig. 2) differs slightly from other teeth of *H. agassizi* in having a relatively broad and more upright primary cusp. The length of the mesial margin of this cusp is not great enough for the tooth to be an upper lateral and this with the large number of crownlets—10—suggests a lower lateral. Further material may show such differences to be within the range of normal variation of the species.

Discussion. The diagnosis by Cappetta (1976) for his *H. agassizi* from the London Clay states that the teeth do not exceed 13 mm in length and that they have from 7 to 10 crownlets including the principal cusp. A tooth from the London Clay figured by Woodward (1886, Pl. 6, fig. 25) under the name *Notidanus serratissimus* is 18 mm in length and has 11 crownlets. Two teeth from South Australia figured by Pledge (1967, Pl. 1, figs. 1, 2) as *'Notidanus' serratissimus* and *'N'.* cf. *serratissimus*, respectively, both exceed 20 mm in length and have 12 crownlets each. These three specimens are included in Cappetta's (1976) synonymy but the discrepancies in size and number of crownlets are not discussed.

The two South Australian localities of Middle and Upper Eocene age are stratigraphically younger than the London Clay which is Lower Eocene. An increase in tooth size of a taxon as the geological age of the specimens decreases has been demonstrated before in sharks' teeth e.g. in *Odontaspis macrota* (Agassiz) from the Lower Tertiaries of Europe and Angola, Darteville and Casier (1943) and Casier (1946, 1966). The South Australian teeth are morphologically similar to those from the London Clay except for their greater size and an increase in the number of crownlets—up to 12 compared with 7 to 10 in the Lower Eocene teeth. This increase is to be expected as such allometric growth patterns are seen in extant hexanchids (see *H. griseus*, above).

Until specimens of either Lower Eocene age from Australia or Middle and Upper Eocene age from Europe, or elsewhere, become available the teeth from South Australia should be included in Cappetta's *H. agassizi.* Additional specimens may show the existence of two fossil species, which, like the dentition of the two extant *Hexanchus* species, are separable primarily on the basis of size.

Distribution. H. agassizi is found in Middle and Upper Eocene beds from South Australia and has been recorded from the Eocene of Russia (Menner, 1928; Glyckman, 1964, *fide* Cappetta, 1976), the Lower Eocene of the London Basin and from North America (Cappetta, 1976).

Genus *Heptranchias* Rafinesque, 1810

Heptranchias Rafinesque, 1810: 13; type species *Heptranchias cinereus* Rafinesque equals *Squalus perlo* Bonnaterre, 1788 (*fide* Bigelow and Schroeder, 1948).

Generic Diagnosis

Seven gill openings; lower labial furrow poorly developed; snout narrow and tapering, length always more than 1·5 x distance between nostrils; horizontal diameter of eye always greater than distance between nostrils.

No central medial tooth in upper jaw; medial tooth in lower jaw with central cusp, which may be asymmetrical; first rows of lower laterals with from 4 to 5 or 6 crownlets; primary cusp markedly bigger than distal crownlets its mesial margin with from 1 to 4 basal denticles. Characters otherwise those of family.

Living Species

One species, *Heptranchias perlo*, of worldwide range. Garrick and Paul (1971) have shown the Australian nominal species *H. dakini* Whitley, 1931 to be conspecific with *H. perlo*. They also note that some New Zealand specimens of *H. perlo* have 6 lateral teeth on each side of the lower jaw compared with the usual 5. Specimens of *H. perlo* from south western Indian Ocean represent an isolated population in that they have very different vertebral counts from those of Australian and Western North Atlantic specimens (Bass *et al.*, 1975).

Heptranchias perlo (Bonnaterre, 1788)

Sharpsnout sevengill shark; Perlon shark
(Plate 13, figure 1)

Squalus perlo Bonnaterre, 1788: 10.

Notidanus cinereus Cuvier, 1829; Günther, 1870: 398; Agassiz, 1843: 218.

Heptranchias perlo (Bonnaterre, 1788); McCulloch, 1911: 2, Pl. 1, fig. 1; McCulloch, 1919: 219, Pl. 16, fig. 4a; McCulloch, 1929: 3; Fowler, 1941: 9; Bigelow and Schroeder, 1948: 88, Figs. 10, 11; Parrott, 1958: 86, text fig.; Applegate and Uyeno, 1968: 197, Pl. 1B; Garrick and Paul, 1971: 1, Pl. 1, 2; Welton, 1974: 6, Fig. 1C, Pl. 1; Bass *et al.*, 1975: 11, Fig. 7, Pl. 4.

Heptranchias dakini Whitley, 1931a: 310; Fowler, 1941: 5; Munro, 1956: 2, Fig. 4; Scott, 1962: 19, text fig.; Whitley, 1968: 5; Scott *et al.*, 1974: 23, text fig.

(non) Heptranchias cf. *perlo* (Rafinesque); Antunes and Jonet, 1969: 131, Pl. 4, fig. 4.

Extant Material Examined. 695 mm female, Victorian coast (AMS I10825) (possible holotype of *H. dakini* Whitley, 1931, see Garrick and Paul, 1971); 720 mm female, off Barrenjoey, N.S.W., Jan., 1955, J. E. Smith (AMS IB3277); 778 mm female, taken at 100 m, N.E. of Cape Solander, N.S.W., 1916, State Trawling Department (AMS I13929); 845 mm male, taken at 120-140 m, 100 km S. of Cape Everard, Victoria, 1910, 'Endeavour' (AMS 110794 (paratype of *H. dakini* Whitley, 1931, see Garrick and Paul, 1971); 720 mm male, taken at 620 m, 56 km S.E. of Newcastle, N.S.W., 33° 11′S, 152° 23′E, 29 Apr., 1971, F.R.V. 'Kapala', prawn trawl (AMS I15975-014); 810 mm female, trawled off Botany Bay, June, 1943, G. P. Whitley (AMS IB1341); 890 mm female, taken at 177 m, 32 km, S.E. Port Stephens, N.S.W., Dec., 1975, 'Kaiyo Maru' (TM D1245); 887 mm female, same data as TM D1245 (TM D1247); 870 mm male, same data as AMS I10794 (NMV E1184).

Dentition

Dental formula of *H. perlo* TM D1245 $\frac{\mathrm{P10\ L8\ M4\ L7\ P9}}{\mathrm{P9\ L5\ M1\ L5\ P10}}$. The number of upper and lower medials is constant while upper laterals may vary between 7 and 9 on each side. As noted above some New Zealand specimens have 6 lower laterals on each side.

Diagnosis. Teeth small with the largest—the 4th or 5th row of lower laterals—not exceeding 25 mm in length, and showing a similar heterodonty to *Hexanchus griseus* but differing significantly in detail.

Upper Jaw

Medials. Crown more finely attenuated, much flatter labio-lingually, more strongly sinuous and curved away from the jaw midline than in *H. griseus.* Similar to *H. vitulus* especially the arcuate distal margin, but crown more inclined and tooth much broader.

Laterals. Primary cusp more slender and relatively much larger than the distal crownlets compared with both extant species of *Hexanchus.* One or 2 small crownlets in first row increasing to 2 to 4 in last row. Mesial margin smooth or with small basal denticles in first row. Subsequent rows with 1 or 2, increasing to 2 or 3, may be 4, basal denticles about equal in size to distal crownlets, i.e. differing markedly from the upper laterals of *H. griseus* and *H. vitulus* which have a finely serrate mesial margin and a greater number of relatively larger distal crownlets.

Lower Jaw

Medial. Tooth with only 2 or 3 cusps on mesial and distal margins, much less inclined than in *H. griseus* and *H. vitulus.* Central cusp relatively larger and approximately symmetrical.

Laterals. Primary cusp about twice as high as first crownlet and more finely attenuated than in *H. griseus* and *H. vitulus* and primary cusp and crownlets more upright than in those species. From 4 to 5 or 6 crownlets in first row to 6 to 8 in last row; crownlets increase in size distally then gradually decrease, the last 2 or

3 in each tooth being markedly smaller than the third or fourth last. This is contrast to the even decrease in size from the first to last crownlet in *Hexanchus* spp. Mesial margin with from 2 to 4 basal denticles in first rows to 1 or 2 in last; basal denticles relatively large, in last rows largest may be almost as big as first crownlet.

Discussion. Bigelow and Schroeder (1948) note a difference in the number of crownlets in the lower laterals between a male and their female specimens. In the present study material this sexual dimorphism is not apparent, the number of crownlets showing a similar range between the two sexes.

The largest tooth seen in the present study is a fifth lower lateral 20 mm in length from a 1340 mm female (NZNM 2180). In a slightly longer specimen, a 1365 mm female, also from New Zealand (CM 418) the fifth lower lateral is only 17·8 mm while the fourth is 19 mm (G. A. Tunnicliffe, pers. comm.). With one exception this is the largest specimen of *H. perlo* seen recorded in the literature. Günther (1870: 398) notes an 'Adult male; stuffed, 7 feet long. From the Antarctic Expedition' under the name *Notidanus cinereus*. This specimen is actually 6 ft 8 in (2030 mm) long, has no teeth, the mouth and gill slits are sewn up and 'it is not possible to identify to species for certain due to its shocking condition' (Mr A. Wheeler, pers. comm.). In light of this Günther's (1870) record for a maximum size of *H. perlo* is regarded as dubious.

Antunes and Jonet (1969) assign a Late Miocene upper right anterior (= medial) hexanchid tooth to *Heptranchias* cf. *perlo*. The thickness of the tooth labio-lingually separates it immediately from Rafinesque's *H. perlo* as does the less sinuous crown and the less curved distal margin.

Garrick and Paul (1971) have shown that the differences between the nominal *H. dakini* Whitley and *H. perlo* (Bonnaterre) are due to sexual dimorphism. The main differences are in the relative position of the dorsal, pectoral and anal fins. In females the anal fin origin is below about the middle of the base of the dorsal fin, in males it is below the end of the dorsal base. Also, the pelvic fin is situated further back in females resulting in a shorter pelvic-anal distance than in males (Garrick and Paul, 1971). In the following Table 1 are compared selected dimensions of one male and two female *H. perlo*. The latter were taken off N.S.W. (TM D1245, TM D1247) while the male was taken off southern Victoria (NMV E1184) by the *Endeavour* in 1910 along with the holo- and paratype of Whitley's *H. dakini*.

Although differing in detail these data demonstrate the same trends of fin placement characteristic of each sex as shown by Garrick and Paul (1971, Table 1).

The two *H. perlo* from off Port Stephens, N.S.W. gave the following vertebral counts:

	TM D1247	TM D1245
Precaudal	93	91
Caudal	56	54
Total	149	145

These counts fall within the range of other Australian and New Zealand specimens of *H. perlo* (Garrick and Paul, 1971) and agree closely with those of three specimens from the western North Atlantic (Springer and Garrick, 1964). They differ from the average counts given by Bass *et al.* (1975) of 75 precaudal and 53 caudal.

Distribution. H. perlo has been recorded from the western and eastern North Atlantic, the Mediterranean, the Cape of Good Hope and Japan (Bigelow and Schroeder, 1948), from Australasia (Garrick and Paul, 1971), from the eastern South Atlantic and southwest Indian Ocean (Bass *et al.*, 1975).

It appears to be a shelf-edge species as it is usually taken at depths between 100-400 m; some specimens have been taken in shallow water—about 50 m—in New Zealand. Shallow water records are probably due to confusion with the broadsnout sevengill genus, *Notorynchus* (Garrick and Paul, 1971). Bass *et al.* (1975) also record *H. perlo* from depths of 50-400 m but note that most were taken from the deeper part of this range.

TABLE 1

Sex and total length	*Catalogue no.*	*% dorsal base anterior to anal fin origin*	*Predorsal length as % tl.*	*Preanal length as % tl.*	*Prepelvic length as % tl.*	*Pelvic origin to anal fin origin as % tl.*
Female 887	TM D1247	82·8	50·2	55·5	41·1	14·4
Female 890	TM D1245	61·6	51·1	55·6	41·9	13·7
Mean of		72·2	50·7	55·6	41·7	14·1
females		93·0	50·3	56·9	40·8	16·1
Male 870	NMV E1184					

Heptranchias howellii (Reed, 1946)
Plate 15, figures 4-7

Notidanion howelli Reed, 1946: 1, figs. 1-3, Fig. 4.

'*Notidanus*' ? *serratissimus* Ag.; Pledge, 1967: 140 *(part.)*, Pl. 1, fig. 3, bottom two specimens (*non* top two specimens).

Heptranchias ezoensis Applegate and Uyeno, 1968: 195, Pl. 1A.

Heptranchias Waldman, 1971: 166, Pl. 1, figs. 1, 2.

Heptranchias howelli (Reed); Welton, 1974: 1, Fig. 1A, B, Pl. 2A, B.

Fossil Material Examined. Four incomplete crowns (RJFJ no. 121; SAM P19573; UAGD F17284).

Occurrence. Blanche Point Marl, Blanche Point, South Australia.

Age. Upper Eocene.

Diagnosis. Based on lower laterals, the only tooth type of this species so far identified. Teeth similar to the extant *H. perlo* but larger, up to 25 mm in length (Waldman, 1971) and with mesial basal denticles, primary cusp and distal crownlets all relatively broader and less attenuated than in the extant species. The primary cusp of *H. perlo* is always relatively higher. *H. howellii* may have up to 5 basal denticles, *H. perlo* from 1 to 4.

Description. Three incomplete crowns (Pl. 15, figs. 4, 5, 7) represent mesial portions of teeth, each having the primary cusp and two crownlets with the second crownlet being characteristically larger than the first. The remaining specimen (Pl. 15, fig. 6) is the distal portion of a tooth with the crownlets increasing in size distally until the last two which decrease, the most distal being very much smaller.

F

Figure 5—Locality map showing occurrences of fossil hexanchid teeth in S.E. Australia.

Discussion. A tooth of *H. howellii* figured by Welton (1974, Pl. 2B) although very close morphologically to an *H. perlo* lower lateral, e.g. row 2 (Pl. 13, fig. 1), still has a more robust shape, a primary cusp not as high and cusp and crownlets inclined and straight rather than inclined and slightly curved as found in the extant species. The other tooth (Welton, 1974, Pl. 2A) is nearer to Reed's (1946, Figs. 1-4) holotype of *H. howellii* and similar to the four incomplete crowns from South Australia.

Reed (1946) did not compare her new species with *H. perlo* but Welton (1974) differentiates *H. perlo* from *H. howellii* on the basis of the former species having a higher primary cusp and no more than 3 basal denticles on the lower laterals. Lower laterals of both left and right rows of two jaws to hand (TM D1245; TM D1247, Pl. 13, fig. 1) have 4 basal denticles on the mesial margin. The main criteria to separate *H. perlo* from *H. howellii* are the higher primary cusp in the extant species, as Welton (1974) notes, but also the generally broader and less attenuated basal denticles, primary cusp and crownlets of *H. howellii*.

Applegate and Uyeno (1968) did not compare their *H. ezoensis* with *H. howellii*. The figured holotype of *H. ezoensis* is very similar to some figured specimens of *H. howellii*, e.g. Pl. 15, fig. 7; Welton (1974, Pl. 2B) except that it has only 2 basal denticles and the primary cusp and crownlets are more inclined. Such differences however are within the normal range of variation seen between the first and last rows of lower laterals of *H. perlo* (Pl. 13, fig. 1) and is in accord with Applegate and Uyeno's own interpretation of the tooth being referable to the fifth lower lateral row. For these reasons *H. ezoensis* is included in the synonymy of *H. howellii*.

The size of teeth of *H. howellii* is comparable to those of *H. perlo* suggesting that the fossil shark too may have grown to a maximum length of less than 2 m. The type specimen is 13 mm in length (Reed, 1946), Welton (1974) records four teeth ranging from 6 mm to 17 mm and Waldman's (1971) two specimens are 19 mm and 25 mm long. The four South Australian fragments are all incomplete but by comparison with the above specimens—measuring from the mesial margin to the apex of the second crownlet—they fall within this size range.

Distribution. Although teeth of *H. howellii* are apparently rare in the fossil record—only about a dozen having been described, including the four in the present study—they are reasonably widespread geographically. In North America they are recorded from the Eocene of New Jersey (Reed, 1946) of Oregon and Washington (Welton, 1974) and British Columbia (Waldman, 1971; Welton, 1974). The tooth from Japan is from the Upper Oligocene (Applegate and Uyeno, 1968) while the South Australian specimens are of Upper Eocene age.

Genus *Notorynchus* Ayres, 1855

Notorynchus Ayres, 1855: 76; type species *Notorynchus maculatus* Ayres, 1855, California.

Generic Diagnosis

Seven gill openings; spiracles small; lower labial furrows well developed; snout broadly rounded, length always less than 1·5 x distance between nostrils; horizontal diameter of eye 2 x or 3 x distance between nostrils; dorsal surface of body and paired fins with small dark splotches, white spots may or may not be present.

Central tooth in both upper and lower jaws, except in some specimens, e.g. off California, which have a variable number of medials either on or either side of the upper symphysis (see below); lower medial without central cusp or, if present, small and strongly asymmetrical; lower laterals with 4 to 7 distal crownlets. Characters otherwise those of family.

Living Species

Possibly only one species *Notorynchus cepedianus* (Péron, 1807) of world-wide range. The taxonomic status of the group at the subgeneric level is particularly confused.

N. macdonaldi Whitley (1931b) was later included by Whitley (1934) himself in the synonymy of *N. cepedianus* when he found than Péron's species had priority. Bass *et al.* (1975) note that the white spots on the dorsal surface of *N. macdonaldi* described by Whitley (1931) had not been reported on further specimens. In fact this coloration seems to be quite widespread as it has been recorded from a number of localities such as Bass Strait (Macdonald and Barron, 1868); New Zealand (Phillips, 1924) and eastern Pacific (no detailed localities given) (Kato *et al.*, 1967). The size of the spots is about that of the eye (Whitley, 1931B; Kato *et al.*, 1967: 6). On the two local specimens caught recently (TM D1291 and TM D1292) the white spots were randomly scattered over the dorsal surface and ranged from 7-30 mm in diameter. Macdonald and Barron (1868) suggested that the spots on their specimen might be the result of disease. An examination of the white spots on the two local specimens revealed no pathological disturbance (B. Munday, pers. comm.)

The presence or absence of a central cusp on the lower medial tooth, the degree of serration of the mesial margin of the lower laterals and the presence or absence of a medial tooth on the symphysis of the upper jaw have been the main criteria used in differentiating the nominal species of *Notorynchus* by a number of authors, for example Günther (1870), Garman (1913), Fowler (1941). The first two characters are variable within the species (see below) but the presence or absence of a tooth on the symphysis of the upper jaw is a difference whose taxonomic status has yet to be established. Many authors such as Agassiz (1835), Müller and Henle (1841), Macdonald and Barron (1864), Garman (1884), Lahille (1928), Whitley (1931), Sadowsky (1970) and Bass *et al.* (1975) either figure or describe in detail the presence of a central upper medial tooth with a single medial on each side.

The issue is confused by some authors, for example Garman (1913), Fowler (1941), who include in the synonymies of their species of *Notorynchus* supposedly lacking an upper central medial, references which actually figure this tooth, for example Agassiz (1835), Müller and Henle (1841). In addition Fowler (1941) includes a number of Australian references in his synonymy of *Heptranchias cepedianus* (Péron), the species supposedly lacking an upper central medial. All Australian specimens so far described in the literature and specimens seen by the present writer possess this tooth. Fowler's single example, *H. cepedianus*, from southern Africa ('Cape Colony coast', Fowler, 1941: 7) was actually a skinned out specimen, thus presumably the jaws were not examined. Bass *et al.* (1975) note that all southern African specimens do possess a tooth on the upper symphysis. Tenore's (1810) description of his new species, *Squalus platycephalus*, from the Mediterranean, gives no clear indication of the number or placement of teeth in the symphyseal area of the upper jaw, 'Superior prominentia intermedia dentibus decem triplici serie dispositis . . .' (Tenore, 1810: 258).

Two sets of jaws of the broadsnout sevengill shark from off the Californian coast recently received at the Tasmanian Museum (see below) have a pair of medials on either side of the upper symphysis. The type of *Notorynchus maculatus* Ayres, 1855 is from California. However, in the description of the teeth of the upper jaw of the type it is not clear whether there is a tooth on the symphysis or not 'Those of the center are narrow, acute, without denticles at the base . . .' (Ayres, 1855: 76-77). Some Californian specimens of *Notorynchus* do have an upper central medial but a range of from 0-2 on each side of the symphysis is known (B. J. Welton, pers. comm.). In the description of tooth types (see below) only the more common condition of three upper medials with one on the symphysis is included as the writer has not seen the complete range of variation present in the Californian specimens. Further detailed comparative studies may show the dental variation of the upper symphyseal area of *Notorynchus* from California and perhaps the Northern Hemisphere in general to be of specific value. If a second species is established and clearly defined only then can the synonymies of this genus be unravelled.

Heptranchias haswelli Ogilby, 1897 was erected on the basis of a set of jaws then in Macleay Museum University of Sydney. Material in this Museum was eventually handed over to the Australian Museum but the type jaws are now lost (J. R. Paxton, L. Bushell, pers. comm.). From the description (Ogilby, 1897) the jaws definitely were of hexanchid (see below) but its status must now remain as a *species inquirenda*.

Notorynchus cepedianus (Péron, 1807)

Broadsnout sevengill shark

(Plate 13, figure 2)

Squalus cepedianus Péron, 1807: 337.
Squalus platycephalus Tenore, 1810: 241, 258.
Notidanus indicus Agassiz, 1835, Pl. E, fig. 1; Agassiz, 1838: 92; Agassiz, 1843: 217; Günther, 1870: 398; Hutton, 1873: 271; Day, 1878; 723, Pl. 189, fig. 4; Johnston, 1882: 138; Johnston, 1890: 38.
Heptanchus indicus Müller and Henle, 1841: 82, Pl. 32.
Notorynchus maculatus Ayres, 1855: 72; Gill, 1862: 495; Herald, 1968: 412.
Notorynchus borealis Gill, 1864: 150.
Heptranchus indicus McDonald and Barron, 1868: 371, Pl. 32, figs. 1-6; Castlenau, 1872: 217; Haswell, 1880: 96; Haswell, 1884a: 88, Pl. 1, fig. 5; Haswell, 1884b: 381, Pl. 10, fig. 1, 2; Ogilby, 1889: 179.
Heptranchus griseus McDonald, 1873: 312.
Notidanus (Heptanchus) indicus McCoy, 1880: 16, Fig. A, B, Pl. 43, fig. 2.
Heptranchias pectorosus Garman, 1884: 56; Lahille, 1928: 299, Figs. 1, 2; Fowler, 1941: 7.
Notorhynchus maculatus Jordan and Evermann, 1896: 17; Jordan and Evermann, 1900, Pl. 2, fig. 7; Welton, 1974: 3, Fig. 1D.
Heptranchias indicus; Waite, 1907: 6; McCulloch, 1911: 2.
Notorhynchus indicus; Zeitz, 1908: 289.
Heptranchias platycephalus (Tenore, 1810); Lahille, 1928: 300, 302.
Notorynchus platycephalus Garman, 1913: 18.
Heptranchias spilotus Lahille, 1913: 26, Figs. 1-3, Pl. 8, fig. 1.
Notorhynchus pectorosus; McCulloch, 1919: 219, Pl. 6, fig. 3a; Waite, 1921: 10, Fig. 5; Waite, 1923: 24, three Figs; Phillips, 1924: 259, Fig. 1.
Notorynchus griseus (McDonald, 1873); McCulloch, 1929: 3.
Notorynchus macdonaldi Whitley, 1931b: 138, Pl. 20, figs. 3-5; Phillips, 1935: 236, Fig. 1.
Notorynchus cepedianus; Whitley, 1934: 181, 197; Whitley, 1940: 70, Figs. 4, 50, 51; Clemens and Wilby, 1946: 51, Fig. 11; Graham, 1953: 62, one Fig.; Scott, 1962: 19, one Fig.; Whitley, 1968: 5; Scott *et al.*, 1974: 23, three Figs; Bass *et al.*, 1975: 14, Fig. 8, Pl. 5.
Heptranchias cepedianus; Fowler, 1941: 6; Parrott, 1958: 84, one Fig.
Notorhynchus cepedianus; Munro, 1956: 2, Fig. 5.
Notorhynchus pectorosus; Garman, 1913: 20; Sadowsky, 1970: 33, Fig. 1.
(non) Heptranchious haswelli; Ogilby, 1897: 62.

Extant Material Examined. 555 mm female, Altona, Vict. (NMV A106); 2391 mm female, mounted specimen (NMV); dried jaws, no data (NMV); 910 mm male, State Fisheries, N.S.W., 1920, no data (AMS 16813); head of specimen taken off Babel Is., N.S.W. at 130 m, 26 June, 1911 (AMS E2161); dried jaws, no data (MUGD); 1520 mm male, Storm Bay, S.E. Tasmania, Safcol (Tas.) Pty. Ltd., May, 1977 (TM D1291); 1648 mm male, same data as TM D1291 (TM D1292) (jaws only of these two specimens retained); dried jaws, 1310 mm immature female, Berkeley Flats, San Francisco Bay, California, U.S.A., B. J. Welton, June, 1976 (TM D1302); dried jaws, 2180 mm immature female, California, U.S.A., B. J. Welton, Jan., 1977 (TM D1303).
Fossil Material Examined. One incomplete tooth (TM Z1991).
Occurrence. Jemmy's Point road cutting, 5 km E of Lakes Entrance, Victoria.
Age. Early Pliocene (Abele *et al.*, 1976).

Dentition

Dental formula of dried jaws, MUGD (Pl. 13, fig. 2): $\frac{\text{P13 L6 M3 L6 P11}}{\text{P9 L6 M1 L6 P8}}$. The number of medials and laterals in both jaws is in most specimens usually constant (except in Californian specimens, see above), but some variation does occur in the laterals, e.g. Bass *et al.* (1975) record one specimen with 7 upper laterals on one side. The 555 mm male from Victoria has

7 lower laterals on the right but the usual 6 on the left. As in *Hexanchus* the number of crownlets, especially in the lower laterals and the degree of denticulation of the mesial margin of all teeth increases with age, and thus the size of the tooth. On the mesial margin of teeth of a given size the basal denticles of *Notorynchus* are larger and more developed than are the serrations of *Hexanchus*. The basal denticles of *Heptranchias* are relatively larger again than those of *Notorynchus*. In both *Notorynchus* and *Heptranchias* the basal denticles extend only half to one-third along the mesial margin, in *Hexanchus* the serrations extend along about two-thirds. The basal denticles of *Heptranchias* are relatively larger again than those of *Notorynchus*.

Diagnosis. Teeth small with the largest—usually the 2nd lower lateral row—probably not exceeding 25 mm in length, and showing a similar heterodonty to *Hexanchus griseus* but differing significantly in detail.

Upper Jaw

Medials. Three rows, the central one of which is on the symphysis and is usually upright but may be slightly inclined to either the right or left. Serrations or basal denticles not usually present on margins of central medial. Basal denticles present on both margins of the two lateral medials but may be absent in juvenile specimens. Crown of medials of *Heptranchias perlo* much more slender and inclined than in *Notorynchus cepedianus*. Root more or less square or slightly tapering basally in outline when viewed labially.

Laterals. Teeth in first rows a little higher than broad ranging through to a little broader than high in last rows. Teeth of *Hexanchus* are lower and broader in comparison. Primary cusp similar to *H. griseus* but with fewer crownlets distally, ranging from only 1 in first row to 4 to 5 or 6 in the last row. Primary cusp and crownlets all relatively broader and larger than in *Heptranchias perlo*.

Lower Jaw

Medial. Tooth similar to that of *Hexanchus griseus* but usually lacking a central cusp. Medials of some specimens, not necessarily large or small, may be quite asymmetrical having one or two more cusps on one side than the other and a strongly oblique central cusp.

Laterals. Teeth about constant breadth and only one-third to one-half broader than high from first to last row. In *Hexanchus* they are about twice as broad as high while in *Heptranchias perlo* they range from a little broader than high in the first row to more than twice as broad as high in the last. Primary cusp with 4 to 6 or 7 basal denticles on mesial margin and 4 to 5 or 6 crownlets which decrease evenly in size distally. Both extant *Hexanchus* species have a greater number of crownlets, from 6 to 12, depending on tooth size, and a serrated mesial margin. *Heptranchias perlo* has about the same number or slightly more than in *Notorynchus cepedianus* but they increase in size distally in the former before decreasing, and then rapidly in the last 1 to 3 crownlets. The primary cusp of *H. perlo* is relatively higher and more attenuated than in the other three species of the family.

Description. Table 2 gives the measurements as per cent of total length of two male topotypes of *N. cepedianus*. Péron's specimen was from Adventure Bay, a bay on Bruny Island which is in Storm Bay, SE Tasmania. No detailed measurements of Australasian material has previously been published to the author's knowledge. Both specimens were light grey above grading to off-white below with numerous dark grey to black splotches about 2-10 mm across on the dorsal surface and paired fins. Also on the dorsal surface of each shark were about a dozen white spots from 7-30 mm diameter, randomly distributed. Dental formula: TM D1291 $\frac{\mathrm{P9\ L6\ M3\ L6\ P11}}{\mathrm{P7\ L6\ M1\ L6\ P8}}$ TM D1292 $\frac{\mathrm{P13\ L6\ M3\ L6\ P11}}{\mathrm{P9\ L6\ M1\ L6\ P10}}$. The lower medial of TM D1291 is symmetrical with no central cusp while in TM D1292 the lower medial is asymmetrical with a very small oblique central cusp.

Discussion. Ogilby (1897) placed his new species of hexanchid in the genus *Heptranchias*, *H. haswelli*, on the basis of a central cusp, inclined to the right, on the lower medial tooth. He also described in the upper jaw:

TABLE 2

Dimensions of *Notorynchus cepedianus* as per cent of total length

		Male *TM D1291*	*Male* *TM D1292*
Total length		*1520 mm*	*1648 mm*
Snout tip to:	outer nostrils	1·3	1·6
	mouth	3·8	3·8
	eye	4·1	4·4
	spiracle	10·2	10·7
	1st gill opening	13·2	13·9
	4th gill opening	15·3	16·3
	7th gill opening	16·0	17·1
	pectoral origin	16·0	17·1
	pelvic origin	41·5	40·1
	dorsal origin	49·2	48·3
	anal origin	54·9	54·3
	upper caudal origin	66·5	66·2
Nostrils:	distance between inner ends	4·4	4·4
	length	1·1	1·2
Eye:	horizontal diameter	1·3	1·3
Mouth:	breadth	12·7	11·8
	height	6·5	6·3
	lower labial furrow	4·4	4·2
Gill openings, length of:	1st	5·6	5·4
	4th	4·9	4·4
	7th	2·8	3·2
Pectoral fin:	outer margin	13·7	13·5
	inner margin	5·7	5·7
	distal margin	11·1	11·4
	length of base	7·6	7·8
Pelvic fin:	origin to lateral lobe	5·7	6·4
	origin to median tip	8·9	10·4
	length of claspers	5·6	6·4
Dorsal fin:	length of base	6·6	7·7
	length of rear tip	2·0	2·3
	vertical height	4·1	4·3
Anal fin:	length of base	4·5	6·0
	length of rear tip	1·6	1·9
	vertical height	2·4	2·7
Caudal fin:	length of upper margin	33·7	34·5
	length of lower margin	8·7	9·4
	base of notch to tip	7·5	6·8
Interspace between bases of:	dorsal and caudal	10·3	10·6
	anal and caudal	7·0	6·0
Distance from origin to origin:	pectorals and pelvics	25·5	23·1
	pelvics and anal	15·5	14·2

- 3 medial teeth, the outer 2 with basal denticles on both margins, the central tooth with entire margins;
- 8 rows of laterals with an increasing number of basal denticles and crownlets from symphysis to articulation, the last 2 rows being lower and broader than the first rows;
- 10 rows of posteriors on each side;

in the lower jaw:

- a medial tooth with an inclined strong central cusp and 4 lateral secondary cusps on each side;
- lateral teeth, the number of which is not given, with 5 to 7 basal denticles on the mesial margin of the primary cusp, followed by 5 to 6 crownlets which decrease regularly in size distally;
- 10 rows of posteriors on each side.

Except for the inclined, strong, central cusp on the lower medial and 8 upper laterals on each side the description is that of *Notorynchus cepedianus*. *Heptranchias perlo* does and both *Hexanchus* species may have a strong central cusp on the lower medial tooth. An asymmettical lower medial in *N. cepedianus* may have a central inclined cusp but in comparison with *Hexanchus* and *Heptranchias* the central cusp could not be called 'strong' (Ogilby, 1897: 63). Eight upper laterals have not been recorded before from *N. cepedianus* but 8 or 9 are common in both *Hexanchus griseus* and *Heptranchias perlo*. Because the type jaws are lost *H. haswelli* must then remain a *species inquirenda*.

An abnormality in the form of bifid teeth (Pl. 14, fig. 3) is noteworthy in that in each case the two 'teeth' both show the basic morphology of *N. cepedianus* teeth. Peyer (1968: 42) tends to 'deny the deeper morphological significance of the presence or absence of accessory cusps'. The anlage, in this case of the first lateral row of the lower jaw of this specimen of *N. cepedianus*, did continue to produce teeth of a morphology characteristic of this species including the basal denticles and the crownlets which decrease evenly in size distally. The mesial 'tooth' has 4 basal denticles on the mesial margin of the primary cusp which is a little larger than the remaining 3 crownlets. The distal 'tooth' which is about one-third the width of the mesial portion, has only 1 basal denticle on the mesial margin of the primary cusp which is noticeably larger than the 3 crownlets. Gudger (1937) noted similar abnormalities in other species of sharks, e.g. *Galeocerdo cuvieri*. The causative mechanism may be a foreign object such as a fish spine being imbedded in the anlage which is subsequently divided as each tooth advances.

The largest definite record of *Notorynchus cepedianus* seen in the literature is that given by Phillips (1935) of a 2888 mm—'9 ft 5·5 in' (Phillips, 1935: 236)—specimen taken in Oriental Bay, New Zealand; the size of the teeth is not recorded. The 2nd lower lateral of the 2391 mm mounted specimen in the National Museum of Victoria is 22 mm in length.

The dental sexual dimorphism in *N. cepedianus* illustrated and noted by Macdonald and Barron (1868) and briefly reiterated by Phillips (1935) has not been seen in any other literature nor in any of the present study material. Indeed, the hand-drawn illustration by Macdonald (Macdonald and Barron, 1868, Pl. 33, fig. 3a, 3d) of the teeth of a female *N. cepedianus*, with the basal denticles of the mesial margins of the lower laterals nearly equal in size to the primary cusp and crownlets, is more akin to teeth of the Upper Cretaceous *N. pectinatus* (Agassiz, 1843: 221; Agassiz, 1844, Pl. 36, fig. 3a; Applegate, 1965b, Figs. 1, 2) than to Péron's extant species and must be regarded as a subjective interpretation of their specimen.

The Early Pliocene tooth (TM Z1991) representing a lower lateral from the 2nd or 4th row is, to the author's knowledge, the first fossil occurrence of this species. Although the basal denticles and the first two crownlets are missing, the tooth, on the basis of the shape of the root and the relative proportions and curvature of the primary cusp and remaining crownlets, can be definitely assigned to the extant species. *N. cepedianus* and *N. primigenius* (see below) were contemporaneous species, but until further fossil specimens of the former species are recognized discussion of their relative geographical distribution would be speculative only.

Distribution. *Notorynchus cepedianus* is recorded from the Pacific Ocean, California to British Columbia (Clemens and Wilby, 1946) and British Columbia to Chile, excluding the tropics (Kato *et al*., 1967), from Japan and Taiwan (Matsubua, 1936 and Chen, 1963, respectively, *fide* Bass *et al*., 1975), from New Zealand (Phillips, 1935) and from Australia, but only from southern waters, e.g. McDonald and Barron, 1868, McCulloch, 1919, Waite, 1921, Scott *et al.*, 1974, no specimens having ever been recorded from northern waters. J. D. Ogilby (*fide* Whitley, 1931) states that *N. cepedianus* does not occur in Queensland waters; the Atlantic Ocean, from Argentina (Lahille, 1928) and Brazil, but not from other parts of the Atlantic (Sadowsky, 1970) and the Indian Ocean (Day, 1878). This report by Day, of a specimen taken off Madras appears to be the most tropical occurrence (about 14° N) of *N. cepedianus*. The broadsnout sevengill shark is commonly taken in shallow coastal waters in South Africa (Bass *et al.*, 1975) and Australia. Phillips (1935) records a 3 m female being taken off a swimming beach in Wellington, New Zealand, but also notes that it is an open ocean shark sometimes entering harbours and inlets. Herald and Ripley (1951) report that while smaller specimens, less than 1·8 m, are common in the shallower waters of San Francisco Bay, larger specimens live in deeper water out of the Bay.

Notorynchus primigenius (Agassiz, 1835)
(Plate 15, figures 8-10)

Notidanus primigenius Agassiz, 1835, Pl. 27, figs. 6-8, 13-17 (*non* figs. 4, 5); Agassiz, 1843: 218; Woodward, 1886: 216, Pl. 6, figs. 19-22; Davis, 1888: 33, Pl. 6, fig. 6; Leriche, 1905: 207, Fig. 62; Chapman, 1914: 271; Leriche, 1926: 388; Leriche, 1927: 8, Pl. 1, fig. 1; Leriche, 1957: 22, Pl. 1, figs. 1-6 (synonymy).

Notidanus marginalis Davis, 1888: 34, Pl. 6, fig. 8 (*non fig.* 7); Chapman, 1914: 268, 271, Fig. 130A; Chapman, 1918: 4, Pl. 6, fig. 8 (?Pl. 9, fig. 1).

Hexanchus cf *griseus* (Bonnaterre); Antunes and Jonet, 1969: 130 *(part.)*, Pl. 4, fig. 3 (*non* figs. 1, 2).

Hexanchus primigenius (Agassiz); Cappetta, 1970: 16, Pl. 4, figs. 11-19.

Fossil Material Examined. Four incomplete crowns (TMZ 1992; NMV P27410, P27411, an unnumbered fragment).

Occurrence. Batesford Limestone, Batesford, Vict. Muddy Creek Marl, Clifton Bank, Muddy Creek, Hamilton, Vict.

Age. Batesford Limestone, Lower Miocene; Muddy Creek Marl, Middle Miocene (Abele *et al.*, 1976).

Diagnosis. Teeth similar to *N. cepedianus* but larger in size, up to 30 mm (Leriche, 1910), and with the primary cusp and crownlets generally straighter and more erect and broader and more robust.

Description. Two specimens (Pl. 15, figs. 8, 9) represent lower lateral teeth, a third specimen (Pl. 15, fig. 10) possibly a lower lateral while a fourth, of only 2 crownlets, cannot be placed in the jaw. One incomplete crown (Pl. 15, fig. 10) consists of a primary cusp with 2 basal denticles—a fracture surface suggests that there were more—and the first crownlet. Both cusp and crownlet are relatively broad, not markedly attenuated and with the cusp about half as high again as the crownlet. The other incomplete crown (Pl. 15, fig. 8) consists of only the primary cusp with 4 basal denticles on the mesial margin. The largest basal denticle is nearly twice the size of the first. The distal portion of a tooth (Pl. 15, fig. 9) has 5 crownlets which evenly decrease in size distally. The root is flat labially with an angular longitudinal ridge on the lingual face about two-thirds up from the base; basal margin very thin labio-lingually.

Discussion. The relatively large, broad primary cusps and crownlets differentiates these fragments from those of both *Hexanchus* and *Heptranchias*. They can be further separated from *Hexanchus* by the relative size difference of the primary cusp and first crownlet; the presence of basal denticles on the mesial margin and cusps and crownlets being more or less straight. In contrast, in *Hexanchus*, the size of the primary cusp is nearer that of the first crownlet; the mesial margin is serrated rather than denticulated and the cusps and crownlets are slightly curved. Additional features separating the fragments from *Heptranchias* are the smallest basal denticle being only about half the size of the biggest and crownlets evenly decreasing in size distally. In contrast, in *Heptranchias*, the smallest basal denticle is only about one-fifth the size of the biggest and the last one or two crownlets decrease rapidly in size from the third or fourth last.

The shape and dimensions of the 2 crownlets of the fourth specimen are conspecific with the other four fragments. All the fragments differ from the extant *N. cepedianus* in their more erect cusp and crownlets. On the basis of the broad, robust and only slightly oblique cusp and crownlets the specimens are assigned to Agassiz's *N. primigenius*. Chapman's (1918) emended description of the lectotype of *Notidanus marginalis* Davis, 1888 is based on an incomplete lateral tooth of a notorynchid. In the figure of the lectotype the primary cusp, which is missing, has been drawn in as a dotted outline, but of a slightly smaller size than the first crownlet. It appears that this interpretation forms the basis for his differentiation (Chapman, 1918: 5) '*N. marginalis* differs essentially in the almost equal size of the two anterior cones, those of *N. primigenius* and *N. serratissimus* being graduated'. Such a character is not found in any hexanchid and as all the characters of the lectotype—the basal denticles showing a small size range and the 6 relatively broad, robust, slightly oblique crownlets decreasing evenly in size distally—are typical of *Notorynchus primigenius, Notidanus marginalis* is here included in that species.

Distribution. *Notorhynchus primigenius* is a widespread fossil species ranging from the Middle Eocene through to the Pleistocene. In Europe it is recorded from the Middle Eocene, Lower Oligocene, Miocene and Pliocene of Belgium (Leriche, 1905, 1910, 1926), from the Miocene of France (Leriche, 1957, Cappetta, 1970), from the Upper Miocene of Portugal as *Hexanchus* cf *griseus* (Antunes and Jonet, 1969) and from the Middle Eocene, Miocene and Pleistocene of England (Woodward, 1886). Davis (1888) and Chapman (1918) note its presence in the Miocene of New Zealand under the name *Notidanus marginalis*.

The occurrence of *Notorynchus primigenius* in the Lower Miocene Batesford Limestone and the Middle Miocene Muddy Creek Formation is the first record of the species from the Australian Tertiary deposits.

Addendum

A jaw of a notorynchid shark (specimen with no number labelled "Cook Strait, *Hexanchus raberi*, 9.5.1944") seen recently in the National Museum, Wellington, New Zealand has the dental formula:

P10—L7—M4—L7—P14.
P11—L6—M1—L6—P10

This occurrence of a *Notorynchus cepedianus* with 4 medial teeth in the upper jaw, outside the Californian coast region, does suggest that such a difference may be due only to individual variation within the species.

A fossil tooth from South Australia recently to hand and referable to *Hexanthus agassizi* Cappetta has been noted by Pledge (pers. comm.; Pledge, N.S., 1977. *Metasqualodon harwoodi* (Sanger, 1887.—A rediscription. Rec. S. Aust. Mus. Adelaide, 17 (17): 285-297, 3 Figs). The tooth (SAM P10867) from the River Murray Cliffis near Wellington is a lower lateral, 20 mm long and 9·4 mm high with 10 crownlets which decrease evenly in size distally and a primary cusp with a denticulated mesial margin. Pledge (1977) shows it to be from the Ettrick Formation which is of Late Oligocene age. This then is the youngest occurrence of *H. agassizi* so far on record.

Acknowledgements

The author wishes to thank Dr O. P. Singleton, University of Melbourne for suggesting the initial project which was the basis of a M.Sc. thesis under his supervision and from which the present study arose. The following people greatly assisted by allowing access to or loan of specimens in their care: Miss J. M. Dixon, National Museum of Victoria; Mr T. F. Flannery, Beaumaris, Victoria; Mr J. M. Lindsay, Department of Mines, South Australia; Dr J. R. Paxton, Australian Museum, Sydney; Mr N. S. Pledge, South Australian Museum, Adelaide and Dr T. H. Rich, National Museum of Victoria. Appreciation is expressed to those who donated specimens, photographs or supplied information especially Dr J. A. Bass previously Oceanographic Research Institute, Durban, South Africa; Dr H. Cappetta, Laboratoire de Paléontologie, Montpellier, France and Mr B. J. Welton previously University of California, Berkeley, U.S.A. and now Natural History Museum, Los Angeles, U.S.A. as well as Mrs L. Bushell, Macleay Museum, University of Sydney, N.S.W.; Mr M. J. Cooper, University of Melbourne; Mr T. A. Darragh, National Museum of Victoria; Professor J. A. F. Garrick, Victoria University of Wellington, New Zealand; Dr. D. F. Hoese, Australian Museum, Sydney; Mr J. M. Morland, National Museum of New Zealand, Wellington; Mr S. Springer, previously Bureau of Commercial Fisheries, U.S.A.; Dr V. G. Springer, United States National Museum, Washington; Mr G. A. Tunnicliffe, Canterbury Museum, Christchurch, New Zealand; Mr D. Ward, London, U.K.; Mr B. F. Webb, Marine Research Laboratories, Taroona, Tasmania and Mr A. Wheeler, British Museum (Natural History), London. Radiographs of two sharks were kindly made by Dr A. J. McIntosh, Hobart, Tasmania and Mr B. Munday, Department of Agriculture, Launceston, Tasmania carried out the pathological examination of the shark skin. Thanks are also due to Mr R. F. Durham, Black Rock, Victoria for his constant enthusiasm and assistance in the initial stages of the photography. Acknowledgement is gratefully made to the Director and Trustees of the Tasmanian Museum for the use of the Museum's time and facilities.

References

ABELE, C. *et al.*, 1976. Tertiary. *In* Douglas, J. G. and Ferguson, J. A. (Eds.) *Geology of Victoria:* i-xi, 1-528. Geological Society of Australia, Special Publication No. 5. Melbourne.

AGASSIZ, L. J. R., 1833-1844. *Research sur les poissons fossiles.* 3: i-viii, 1-390, Atlas: 1-34, 83 pls. Neuchâtel.

ANTUNES, M. T. and JONET, S., 1969. Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. *Rev. Fac. Ciênc. Lisboa,* (2, C) 16 (1): 119-280, 14 Figs., 20 pls.

APPLEGATE, S. P., 1965a. Tooth terminology and variation in sharks with special reference to the sand shark *Carcharias taurus* Rafinesque. *Contr. Sci., Los Angeles Co. Mus.* 86: 1-18, 5 Figs.

————, 1965b. A confirmation of the validity of *Notorhynchus pectinatus*; the second record of this Upper Cretaceous cowshark. *Bull. Sth. Calif. Acad. Sci.* 64, (3): 122-126, 1 Fig.

———— and T. UYENO, 1968. The first discovery of a fossil tooth belonging to the shark genus *Heptranchias*, with a new *Pristiophorus* spine, both from the Oligocene of Japan. *Bull. Nat. Sci. Mus. Tokyo* 11(2): 195-200, 1 pl.

AYRES, W. O., 1855. *Notorynchus maculatus*—Ayres. *Proc. Calif. Acad. Sci.* 1: 76-77.

BASS, A. J., J. D. D'AUBREY and N. KISTINASAMY, 1975. Sharks of the east coast of southern Africa. *v.* The families Hexanchidae, Chlamydoselachidae, Heterodontidae, Pristiophoridae and Squatinidae. *Invest. Rep. oceanogr. Res. Inst.,* Durban (43): 1-50, 8 pls.

BIGELOW, H. B. and W. C. SCHROEDER, 1948. Fishes of the Western North Atlantic, I. Lancelets, Cyclostomes, Sharks. *Mem. Sears. Fdn. mar. Res.,* New Haven, 1: 1-576, 106 Figs.

BONNATERRE, J. P., 1788. *Tableau encyclopédique et methodique, Ichthyologie.* Paris: i-vi, 1-215, 102 pls.

CAPPETTA, H., 1970. Les sélaciens du Miocène de la région de Montpellier. Mem Ext. *Palaeovertebrata,* Montpellier: 1-139, 22 Figs.: 1-19, 27 pls.

————, 1975. Sélaciens et Holocéphale du Gargasien de la région de Gargas (Vaucluse). *Géol. Méditerr.,* Aix-en-Provence, 2(3): 115-134, 10 Figs., 2 pls.

————, 1976. Selaciens nouveaux du London Clay de l'Essex (Ypresien du Bassin de Londres). *Geobios,* Lyon, 9(5): 551-575, 1 Fig., 4 pls.

CASIER, E., 1966. Faune ichthyologique du London Clay. *Brit. Mus. (Nat. Hist.)*: 1-496, 82 Figs., 68 pls.

CASTELNAU, F. L., 1872. Contribution to the ichthyology of Australia. *Proc. Zool. Acclim. Soc. Vict.* 1: 29-248.

CHAPMAN, F., 1914. *Australasian Fossils:* 1-341, 150 Figs. Melbourne.

————, 1918. Descriptions and revisions of the Cretaceous and Tertiary fish-remains of New Zealand. *Palaeont. Bull.,* Wellington, 7: 1-45, 9 pls.

CLEMENTS, W. A. and G. V. WILBY, 1946. Fishes of the Pacific Coast of Canada. *Bull. Fish. Res. Bd. Can.* 68: 1-368, 253 Figs.

DAVIS, J. W., 1888. The fossil fish remains from the Tertiary Formations of New Zealand. *Sci. Trans. R. Dubl. Soc.,* Dublin (2), 4: 1-48, 7 pls.

DAY, F., 1878. *The fishes of India.* London, 1: 1-778, 2, 198 pls.

FOWLER, H. W., 1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. *Bull. U.S. natn. Mus.,* Washington, (100) 13: 1-879.

GARMAN, S., 1884. A species of *Heptranchias* supposed to be new. *Bull. Essex. Inst.* 16: 56-57.

————, 1913. The Plagiostomia (Sharks, Skates and Rays). *Mem. Mus. Comp. Zool. Harvard* 36: 1-528, 77 pls.

GARRICK, J. A. F. and L. J. PAUL, 1971. *Heptranchias dakini* Whitley, 1931, a synonym of *H. perlo* (Bonnaterre, 1788), the sharpsnouted sevengill or Perlon shark, with notes on sexual dimorphism in this species. *Zoology Publs. Vict. Univ. Wellington* 54: 1-14.

GILL, T., 1864. Second contribution to the Selachology of California. *Proc. Acad. nat. Sci. Philad.* 16: 147-151.

GRAHAM, D. H., 1953. *A treasury of New Zealand fishes*. Wellington: 1-404.

GUDGER, E. W., 1937. Abnormal dentition in sharks, Selachii. *Bull. Am. Mus. nat. Hist.*, New York, 72(2): 249-280, 21 Figs.

GÜNTHER, A., 1870. Subclass IV. Chondropterygii. *In*: Catalogue of the Phystomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegesidae, and of the Lophobranchii, Plectognathi, Dipnoe, Ganoidei, Chondropterygii, Cyclostomata, Leptocardii, in the British Museum. London: 1-549.

HASWELL, W. A., 1880. Notes on *Galeocerdo rayneri* with a list of other sharks taken in Port Jackson. *Proc. Linn. Soc. N.S.W.* 5: 95-97, 1 pl.

————, 1884a. Studies on the elasmobranch skeleton. *Proc. Linn. Soc. N.S.W.* 9(1): 71-119, 1 pl.

————, 1884b. Note on the claspers of *Heptanchus. Proc. Linn. Soc. N.S.W.* 9(2): 381-382, 1 pl.

HERALD, E. S., 1951. The relative abundance of sharks and bat stingrays in San Francisco Bay. *Calif. Fish Game* 37(3): 315-329.

HOOIJIER, D. A., 1954. Pleistocene vertebrates from Celebes. Elasmobrabranch. *Proc. K. Ned. Akad. Wet.*, Leiden, (B), 57: 475-485, 2 pls.

HUTTON, F. W., 1873. Contributions to the ichthyology of New Zealand. *Trans. N.Z. Inst.* 5: 259-272.

Johnston, R. M., 1882 (1883). The fishes of Tasmania. *Pap. R. Soc. Tasm.*: 54-153.

————, 1890 (1891). Further observations upon the fishes and fishing industries of Tasmania, together with a revised list of indigenous species. *Pap. R. Soc. Tasm.*: 22-46.

JORDAN, D. S., 1907. The fossil fish of California with supplementary notes on other species of extinct fishes. *Univ. Calif. Publs. Bull. Dep. Geol.*, Berkeley, 5(7): 95-144, 2 pls.

———— and B. W. EVERMANN, 1896. The fishes of North and Middle America. *Bull. U.S. natn. Mus.*, Washington, 47(1): I-LX, 1-1240.

————, 1900. The fishes of North and Middle America. *Bull. U.S. natn. Mus.*, Washington, 47(4): I-CI, 3137-3313, 392 pls.

KATO, S., S. SPRINGER and M. H. WAGNER, 1967. Field guide to Eastern Pacific and Hawaiian sharks. *Circ. Fish Wildl. Serv. Wash.* 271: 1-47, 75 Figs.

KEMP, N. R., 1970. *Studies on the dentition of Australian Tertiary and Recent sharks.* Unpublished M.Sc. thesis, University of Melbourne: 1-354, 63 pls.

LAHILLE, F., 1913. Nota sobre los géneros *Heptranchias y Hexanchus. An. Mus. nac. B. Aires.* 18: 25-32. 3 Figs., 2 pls.

————, 1928. Nota solore unos peces elasmobranquios. *An. Mus. nac. B. Aires* 34: 299-340, 27 Figs., 5 pls.

LERICHE, M., 1905. Les poissons éocène de la Belgique. *Mem. Mus. r. Hist. nat. Belg.*, Bruxelles, 3(11): 49-228, 9 pls.

————, 1910. Les poissons oligocènes de la Belgique. *Mem. Mus. r. Hist. nat. Belg.*, Bruxelles, 5: 229-363, 27 pls.

————, 1926. Les poissons néogène de la Belgique. *Mem. Mus. r. Hist. nat. Belg.*, Bruxelles, 32: 368-472, 14 pls.

————, 1927. Les poissons de la Molasse suisse. *Abh. Schweiz. paläont. ges.*, Basel, 46: 1-56, 7 pls., 47: 57-120, 7 pls.

————, 1957. Les poissons néogènes de la Bretagne de l'Anjou et de la Touraine. *Mem. Soc. geol. Fr.*, Paris, (5) 81: 1-64, 4 pls.

LYNCH, D. D., 1963. First Australian record, *Hexanchus griseus* (Bonnaterre, 1780). The Six-gilled Shark. *Mem. Natn. Mus. Vict.* 26: 259-260, 1 pl.

MCCOY, F., 1880. *Prodromus Zool. Vict.*, Melbourne 5: 1-58, 10 pls.

MCCULLOCH, A. R., 1911. Report on the fishes obtained by the F.I.S. 'Endeavour' on the coasts of New South Wales, Victoria, South Australia and Tasmania. *Zool. Res. Endeavour* 1(1): 1-87, 26 pls.

————, 1919. Check-list of the fish and fish-like animals of New South Wales. Part i. *Austr. Zool.* 1(7): 217-229, 3 pls.

————, 1929. A check-list of the fishes recorded from Australia. *Aust. Mus. Mem.* 5(1): 1-144.

MACDONALD, J. D., 1873. A communication . . . containing descriptions of two sharks taken off Flinders Island, Bass's Straits, during the voyage of H.M.S. 'Herald' in the South Seas. *Proc. Zool. Soc.* (Lond.): 312.

MACDONALD, J. D. and C. BARRON, 1868. Notes on *Heptranchus indicus*, chiefly as regards sexual characters. *Proc. Zool. Soc.* (Lond.): 371-373, 1 pl.

MÜLLER, J. and F. G. HENLE, 1841. *Systematische Beschreibung der Plagiostomen.* Berlin: i-xxii, 1-200, 60 pls.

MUNRO, I. S. R., 1956. Handbook of Australian fishes. *Fisheries Newsletter*, Australia, 1: 1-8, 56 Figs.

OGILBY, J. D., 1889. List of the Australian *Palaeichthyes*, with notes on their synonymy and distribution. *Proc. Linn. Soc. N.S.W.* 4(1): 178-186.

————, 1897. New genera and species of Australian fishes. *Proc. Linn. Soc. N.S.W.* 22(1): 62-95.

PARROTT, A. W., 1958. *Big game fishes and sharks of New Zealand*: 1-127. London.

PATTERSON, C., 1967. Classes Selachii and Holocephali. *In* W. B. Harland *et al.* (Eds.) *The Fossil Record*. London (Geological Society): 666-675.

PERON, F., 1807. *Voyage de Decouverts Aux Terres Australes*. 1: 1-496. Paris.

PEYER, B., 1968. *Comparative Odontology*. R. Zangerl, Trans. and Ed.: 1-347, 95 pls. Chicago and London.

PHILLIPS, W. J., 1924. A review of the elasmobranch fishes of New Zealand, *N.Z. J. Sci. Tech.* 6(5-6): 257-269, 14 Figs.

————, 1935. Sharks of New Zealand; No. 4, *N.Z. J. Sci. Tech.* 16: 236-241, 3 Figs.

PLEDGE, N. S., 1967. Fossil elasmobranch teeth of South Australia and their stratigraphic distribution. *Trans. R. Soc. S. Aust.* 91: 135-160, 4 pls.

RAFINESQUE, C. S., 1810. *Caratteri di alcuni nuovi generi e nuovi specie de animali (Presci) . . . della Sicilia*: 1-105, 20 pls. Palerme.

REED, M. D., 1946. A new species of fossil shark from New Jersey. *Notul. Nat.*, Philadelphia, 172: 1-3, 1 pl.

SADOWSKY, V., 1970. First record of broad-snouted seven-gilled shark from Cananéia, coast of Brazil. *Bolm Inst. oceanogr. S. Paulo* 18(1): 33-35, 1 Fig.

SCOTT, T. D., 1962. *The marine and fresh water fishes of South Australia*. Adelaide: 1-338.

————, C. J. M. GLOVER and R. V. SOUTHCOTT, 1974. *The marine and fresh water fishes of South Australia*. Adelaide: 1-392.

SPRINGER, S. and R. A. WALLER, 1969. *Hexanchus vitulus*, a new sixgill shark from the Bahamas. *Bull. mar. Sci.* 19(1): 159-174.

SPRINGER, V. G. and J. A. F. GARRICK, 1964. A survey of vertebral numbers in sharks. *Proc. U.S. natn. Mus.*, Washington, 116: 73-96.

TENORE, M., 1810. Sopra una nuova specie di Squadro pescato nelle acque della riviera di Chiaja del littorale di Napoli. *Mem. Acad. Pont.* Naples, 1: 241-265.

WAITE, E. R., 1907. A basic list of the fishes of New Zealand. *Rec. Cantab. Mus.*, Christchurch, 1: 3-39.

————, 1921. Catalogue of the fishes of South Australia. *Rec. S. Aust. Mus.*, Adelaide, 2: 1-208, 332 Figs., 1 pl.

————, 1923. *The Fishes of South Australia*. Adelaide: 1-243.

WALDMAN, M., 1971. Hexanchid and orthacodontid shark teeth from the Lower Tertiary of Vancouver Island, British Columbia. *Can. J. Earth Sci.* 8(1): 166-170.

WELTON, B. J., 1974. *Heptranchias howellii* (Reed, 1946) (Selachii: Hexanchidae) in the Eocene of the United States and British Columbia. *Paleobios*, Berkeley, Calif., 17: 1-15, 2 Figs., 2 pls.

WHITLEY, G. P., 1931a. New names for Australian fishes. *Austr. Zool.* 6: 310-334, 1 Fig., 3 pls.

————, 1931b. Studies in ichthyology, No. 5 *Rec. Austr. Mus.*, Sydney, 18(4): 138-160, 2 Figs., 2 pls.

————, 1934. Notes on some Australian sharks. *Mem. Qd. Mus.*, Brisbane, 10(4): 180-200, 4 Figs., 3 pls.

————, 1940. *The fishes of Australia. Part 1. The sharks, rays, devil fish and other primitive fishes of Australia and New Zealand*. Sydney (Royal Zoological Society): 1-280, 302 Figs.

————, 1968. A check-list of the fishes recorded from the New Zealand region. *Austr. Zool.* 15(1): 1-102.

WOODWARD, A. S., 1886. On the palaeontology of the Selachian genus *Notidanus* Cuvier. *Geol. Mag.*, London (3) 3: 205-217, 253-259, 1 pl.

ZEITZ, A. A synopsis of the fish of South Australia. Part 1 *Trans. R. Soc. S. Aust.* 32: 288-293.

Explanation of Plates

All photographs by the author

PLATE 12

Figures 1-4—*Hexanchus griseus* (Bonnaterre). Teeth *in situ* of 4250 mm specimen from N.S.W. (AMS I19110-001).

1. Photomontage of labial view of replacement series of right side of upper and lower jaws including medial rows of left side of upper jaw and lower medial row. Functional series of upper jaw is seen inciso-lingually.
2. Incisal and labial views of functional series of medial rows of upper jaw. Note basal denticles on medial margin especially of first right medial row (x1).
3. Labial view of replacement series of medial rows of upper jaw. Note large basal denticles on distal margins of first right (apex of crown broken) and second left medial teeth. First left row is almost obscured due to shrinkage of jaw in symphyseal region (x1).
4. Lower medial replacement row. Note first tooth with bifurcated central cusp while second tooth has no central cusp (x1).

Figure 5—*Hexanchus vitulus* (Springer and Waller). Labial view of teeth of 1550 mm male from Natal, South Africa; right side of upper and lower jaws including lower medial tooth. From Bass *et al.*, 1975, with permission.

PLATE 13

Figure 1—*Heptranchias perlo* (Bonnaterre). Labial view of teeth of 887 mm female from N.S.W.; right side of upper and lower jaws including lower medial tooth; posteriors, except for first upper, are not shown (TM D1247).

Figure 2—*Notorynchus cepedianus* (Péron). Labial view of teeth of right side of upper and lower jaws including upper central and lower medial teeth; posteriors, except for first upper, are not shown (NMV).

PLATE 14

Figures 1-3—*Notorynchus cepedianus* (Péron).

1. Symphyseal area of upper jaw of specimen from California, U.S.A. showing medial and first lateral rows. Note two medial rows on either side of symphysis (TM D1303) (x1·5).
2. Symphyseal area of upper jaw of specimen—topotype—from Storm Bay, S.E. Tasmania showing medial and first lateral rows. Note central medial row on the symphysis (TM D1291) (x2).
3. Abnormal, bifid tooth of first lateral row of lower jaws (NMV) (x2).

Figures 4-11—*Hexanchus agassizi* (Cappetta).

4-8 From Naracoorte No. 5 Bore, 135-145 m (x2).

4. Upper lateral, labial face, lingual face (SAM P19552a).
5. Upper lateral, labial face, lingual face (SAM P19552b).
6. Upper lateral, labial face, lingual face (SAM P19552c).
7. Lower lateral, labial face, lingual face (SAM P19552d).
8. Lower lateral, labial face, lingual face (SAM P19552e).
9. Lower lateral, labial face, lingual face. Blanche Point Marl (RJFJ no. 121a) (x2).

10-11. Lower lateral, Blanche Point Marl (RJFJ no. 121b).

10. Labial face, lingual face (x2).
11. Labial face; note basal denticle on first crownlet (x12).

PLATE 15

(all teeth x2)

Figures 1-3—*Hexanchus agassizi* Cappetta.

1. Lower lateral, labial face, lingual face, Naracoorte No. 5 Bore, 135-145 m (SAMD V34).
2. Lower lateral, labial face, lingual face, Blanche Point Marl (UAGD F17262).
3. Lower lateral, labial face, lingual face, London Clay, Isle of Sheppey, U.K.; for comparison (NRK).

Figures 4-7—*Heptranchias howelli* (Reed). Lower laterals, labial face, lingual face, Blanche Point Marl.

4. (SAM P19572).
5. (UAGD F172284a).
6. (UAGD F17284b).
7. (SAM P19573).

Figures 8-10—*Notorynchus primigenius* (Agassiz). Lower laterals, labial face, lingual face.

8. Muddy Creek Marl (TFF).
9. Batesford Limestone (NMV P27411).
10. Batesford Limestone (NMV P27410).